

Concentration of bat activity in riparian habitats over an elevational gradient

S.D. Grindal, J.L. Morissette, and R.M. Brigham

Abstract: Riparian areas are generally assumed to represent important foraging areas for insectivorous bats, but this contention has rarely been formally quantified. To test this assumption, we used bat detectors to compare the relative activity levels of a community of temperate-zone bat species between riparian (lake) and upland (cutblock) habitats at three different elevations (ranging from 540 to 1800 m) in a forested area of southern British Columbia. In addition, we also investigated the sex and age class distributions of bats (based on mist-net captures) between riparian and upland habitats among the elevational zones. Bat activity levels were significantly greater in riparian than upland areas (10 and 40 times greater for foraging and commuting activity, respectively). Capture rates were greater in riparian areas and biased towards females, suggesting that female bats may preferentially select riparian areas, probably because of the abundant prey resources typically associated with this habitat. Captures of females also predominated at lower elevations, whereas males were captured more often in higher elevation zones. Our data support the assumption that riparian habitats represent important foraging and probably drinking areas for bats. The sex bias and differences in capture rates and activity levels need to be considered when designing bat surveys in different habitat types or over elevational gradients.

Résumé : Les rives sont généralement considérées comme d'importantes zones d'alimentation pour les chauves-souris insectivores, mais cette supposition n'a jamais été formellement vérifiée quantitativement. Pour éprouver l'hypothèse, nous avons utilisé des détecteurs de chauves-souris permettant de comparer l'importance relative de l'activité d'une communauté d'une espèce de zone tempérée en zone riparienne (d'un lac) et en région montagneuse (dans une parcelle), à trois altitudes différentes (de 540 à 1800 m), dans une zone forestière du sud de la Colombie-Britannique. Nous avons également évalué la répartition des chauves-souris (capturées au filet japonais) en classes d'âge et de sexe dans les zones riparienne et montagneuse à chaque altitude. L'activité des chauves-souris est significativement plus intense (10 fois plus dans le cas de la recherche de nourriture et 40 fois plus dans le cas des déplacements) en zone riparienne qu'en montagne. Les taux de capture sont plus élevés en zone riparienne, particulièrement chez les femelles, ce qui semble indiquer que les femelles choisissent les rives par préférence, probablement à cause de l'abondance des proies associée à cet habitat. Les captures de femelles ont également été plus abondantes à basse altitude, alors que les mâles ont été capturés plus souvent en zone élevée.

[Traduit par la Rédaction]

Introduction

In many studies of the foraging behaviour of insectivorous bats, the focus has been on study sites located in riparian areas (e.g., Anthony and Kunz 1977; Racey and Swift 1985; Jones and Rayner 1988; Brigham 1991; Saunders and Barclay 1992; Barclay and Brigham 1994; Hayes and Adams 1995; Rautenbach et al. 1996; Walsh and Harris 1996; Vaughan et al. 1997; Wilkinson and Barclay 1997). Arguably, this bias towards studies in riparian areas is the result of a long-held assumption that insectivorous bats concentrate their activity in these habitats. Another consequence of this assumption is that sampling efforts (e.g., netting, ultra-

sonic detectors, direct observations) have been largely concentrated in riparian areas (Kunz 1988).

It is generally assumed that riparian areas support high concentrations of insect prey that are attractive to, and therefore support, high densities of foraging bats (Racey and Swift 1985; Brigham and Fenton 1991). To date, however, there have been few direct quantitative evaluations of the assumption that bat activity levels are consistently higher over lakes or calm streams relative to nonriparian areas or of the magnitude of any differences in activity levels (Geggie and Fenton 1985; Furlonger et al. 1987). This is especially true of relatively intact forested habitats (Brigham 1995). A consistently high prey density coupled with the acoustically simple environment above water (Kalko and Schnitzler 1993; Barclay and Brigham 1994; Brigham et al. 1997) should make riparian areas good foraging habitats. From the perspective of bats, a high-quality riparian area is calm, slow-moving water. Von Frenckell and Barclay (1987) and Mackey and Barclay (1989) showed that noise created by fast-flowing water interfered with bats' echolocation, resulting in these riparian areas being rarely used by foraging bats.

Bat activity has been documented to be greater at lower elevations (Thomas 1988; Barclay 1991). This is probably

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S.D. Grindal,¹ J.L. Morissette, and R.M. Brigham.
Department of Biology, University of Regina, Regina, SK
S4S 0A2, Canada.

¹Author to whom all correspondence should be sent at the following address: Suite 600, 555 Fourth Avenue S.W., Calgary, AB T2P 3E7, Canada (e-mail: sgrindal@axys.net).

due to the higher temperatures and higher insect densities that typically occur at lower elevations (Grindal and Brigham 1999). Higher temperatures should also allow reproductive female bats to maintain a high body temperature, which facilitates embryo development (Racey 1973). In contrast, adult males, juveniles (both sexes), and nonreproductive adult females may seek higher elevations with lower temperatures so that they can more readily enter torpor and thus conserve energy (Barclay 1991; Hamilton and Barclay 1994).

We feel that in order to design and interpret data from bat studies it is important to evaluate the assumption that riparian areas are important for foraging bats, as well as how elevation may affect the distribution of bats. This is especially true in situations where bats roost and forage under natural conditions (i.e., forests) and bat behaviour is likely less affected by the availability of man-made structures for roosting (Brigham and Fenton 1986) or the presence of streetlights, which attract concentrations of insects (e.g., Geggie and Fenton 1985; Furlonger et al. 1987; Hickey and Fenton 1990; Rydell 1992).

The purpose of our study was to compare the relative activity levels (using bat detectors) of a community of temperate-zone bat species between riparian (lake) and upland (cutblock) habitats over an elevational gradient. We sampled cutblocks because, except for the lack of water, they are structurally similar to riparian habitats in that they are relatively open and uncluttered, and because activity levels are exceptionally low within forest habitats (Grindal and Brigham 1999). Although cutblocks would not be considered "natural" habitats, Grindal (1996) showed that bat activity was no different in cutblocks versus natural openings (avalanche chutes). In addition, we investigated the sex and age class distributions of bats (based on mist-net captures) between riparian and upland habitats and among elevational zones. We predicted that bat activity levels and capture rates would be greater in riparian areas and at lower elevations relative to upland areas and higher elevations. Furthermore, we predicted that greater numbers of reproductively active adult females than adult males would be captured in riparian areas and at lower elevations, owing to the greater energetic demands on females, as well as the need to maintain high body temperatures to facilitate embryo development and milk production (Barclay 1991).

Methods

The study took place 20 km east of Nelson (117°05'W, 49°38'N) in the southern interior of British Columbia during the summers of 1993, 1994, and 1995. Bat activity levels were compared between riparian and upland habitats among three elevational zones: low (540–1000 m), mid (1000–1400 m), and high (1400–1800 m). The low and mid elevational zones were composed of mixed conifer forests dominated by western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). The high elevational zone was dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). A progressively higher elevational zone was accompanied by an increase in the mean summer precipitation range (low, 201–230 mm; mid, 231–300 mm; high, 301–400 mm) combined with a decrease in the mean summer temperature range (low, 7.1–10.0°C; mid, 7.1–10.0°C; high, <7.0°C; Braumandl and Curran 1992).

Monitoring of echolocation calls

We monitored bat activity using Mini-2[®] ultrasonic bat detectors (Ultra Sound Advice, London, U.K.) for 90 min immediately after sunset. To control for effects of environmental clutter on bat activity (Brigham et al. 1997), detectors were placed in habitat of similar physical structure (i.e., edges and openings) in the two different habitat types (riparian and upland). We placed detectors with the microphone oriented upwards at least 50–75 m into the center of each habitat type and along the forest edge in each habitat type. To sample the center of lakes, we deployed detectors in plastic containers mounted on small floating inflatable tubes that were anchored to the shore using guy lines. At all other sites, detectors were placed on 1 m long poles. All detectors were connected to tape recorders, which permitted remote sampling. We chose sampling sites where vegetation (mature forest >80 years old) created a distinct structural edge along lake shorelines or cutblock boundaries.

At each sampling site, we used two bat detectors, one tuned to 25 kHz and the other to 40 kHz. The use of these two frequencies permitted the detection of the echolocation calls of most of the bat species expected or known to occur in the study area (*Myotis californicus*, *M. evotis*, *M. lucifugus*, *M. septentrionalis*, *M. thysanodes*, *M. volans*, *M. yumanensis*, *Corynorhinus townsendii*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus cinereus*; Nagorsen and Brigham 1993), although precise species identification was not possible. Because of differing intensities and frequencies of echolocation calls, activity by some species (e.g., *C. townsendii*) was likely underestimated.

Bat activity was separated into two types: commuting and foraging. A commuting pass was identified by two or more consecutive pulses representing travel or prey-seeking activity by bats (Thomas 1988). A foraging attempt was identified by a rapid series of echolocation calls (i.e., feeding buzzes) emitted when bats make a foraging attempt (Griffin et al. 1960).

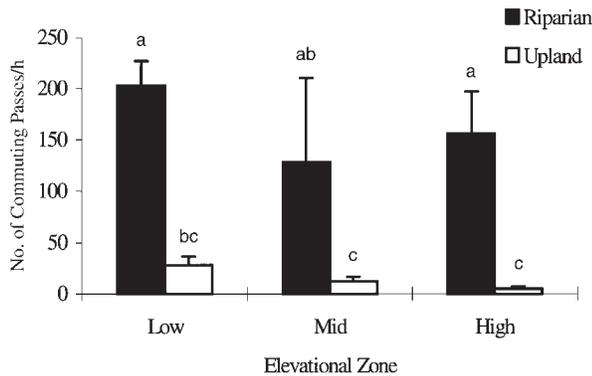
Bat activity was sampled at three different lakes (each approximately 10–15 ha in size) in each of the mid and high elevational zones. Three different locations (at least 2 km apart) along the western arm of Kootenay Lake (>25 km long, >1 km wide) were used as the "lake sites" in the low elevational zone. At least four different cutblocks (mean 57 ha, range 12–116 ha) that had been recently harvested (<20 years since harvest) were sampled in each elevational zone. See Grindal and Brigham (1999) for more details of cutblock-sampling methodology.

Independent riparian (in 1995) and cutblock (in 1993 and 1994) samples were collected in all three elevational zones at monthly intervals throughout the summer (June, July, August). In July 1994, riparian sampling was conducted at the same high-elevation lakes (although at different locations within the lakes), potentially limiting the independence of samples. Although most riparian and upland sites were not sampled concurrently within the same year, the results of sampling conducted for both habitats in the same year (i.e., 1994) were indicative of the overall results. Additionally, there were no significant differences between years in cutblock (commuting: $F_{[1]} = 0.08$, $p = 0.2$; foraging: $F_{[1]} = 0.6$, $p = 0.5$) or riparian areas (commuting: $F_{[1]} = 1.7$, $p = 0.2$; foraging: $F_{[1]} = 0.1$, $p = 0.7$). Sampling occurred only on warm nights (>10°C at sunset) with no precipitation.

Bat capture

To assess differences in sex and age class distributions, we captured bats using mist nets set for a minimum of 2 h after sunset in riparian (e.g., along lake edges, over slow-flowing creeks) and upland (e.g., along cutblock edges, over roads) habitats in all three elevational zones. Upland mist-netting sites were distinguished from riparian sites by being at least 500 m from major water bodies or creeks (>1 m in width).

Fig. 1. Commuting activity levels (mean + 1 SE) of bats in riparian and upland habitat over three elevational zones. Means with different letters are significantly different ($p < 0.05$).



Captured bats were identified to species, sexed, and aged (adult or juvenile), then released at the point of capture. We characterized the reproductive condition of adult females as either pregnant (estimated by palpation of the abdomen), lactating (swollen pink nipples), nonpregnant (unswollen, furred nipples), or postlactating (unswollen, bare nipples; Racey 1988). Juvenile status was determined from incomplete ossification of the third metacarpal-phalangeal joint (Anthony 1988).

Statistical analyses

Two-way analysis of variance (Zar 1984) was used to examine the effect of habitat type and elevational zone on commuting and foraging activity. Where effects were significant, we conducted Tukey's multiple comparisons (Zar 1984). We combined the activity data collected for lake center and lake/forest edge areas and likewise for cutblock center and cutblock/forest edge areas. Because sample sizes were small, bat species were also pooled for comparisons using age, sex, and reproductive class.

Chi-squared tests were used to test for differences between sex and age classes of bats captured between low and mid elevational zones, as well as between riparian and upland habitats. We used captures per mist-net hour (1 mist-net hour = one 2.5×6 m net operated for 1 h) in our analyses to control for unequal sampling effort. For purposes of analysis, captured adult females were separated into two groups: pregnant or lactating (P/L); and nonpregnant or postlactating (NP/PL). Use of these two groups differentiates between reproductive and nonreproductive females, respectively, at the time of capture. For all statistical analyses we used an α level of 0.05.

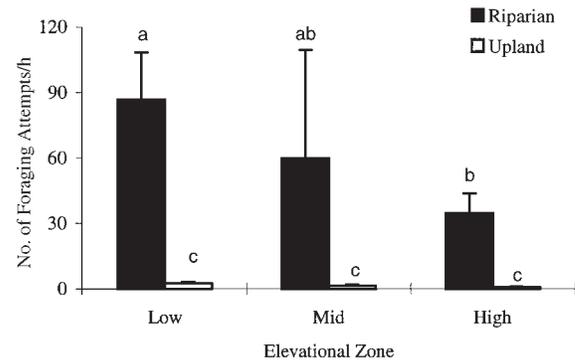
Results

Monitoring of echolocation calls

We sampled nine different lake locations on 12 nights: three lakes in the high elevational zone in 1994 and three lakes in each of the three elevational zones in 1995. From this sampling effort, we detected 2961 commuting passes and 1008 foraging attempts. Cutblocks were sampled on 77 nights in 1993 and 1994, resulting in 2024 commuting passes and 192 foraging attempts.

Both habitat type and elevation had a significant effect on commuting activity (habitat: $F_{[1]} = 103.8$, $p < 0.001$; elevation: $F_{[2]} = 3.2$, $p = 0.04$) and foraging activity (habitat: $F_{[1]} = 132.3$, $p < 0.001$; elevation: $F_{[2]} = 8.5$, $p = 0.0003$). Further, there was a significant interaction between habitat type and elevation for foraging activity ($F_{[2]} = 8.5$, $p =$

Fig. 2. Foraging activity levels (mean + 1 SE) of bats in riparian and upland habitat over three elevational zones. Means with different letters are significantly different ($p < 0.05$).



0.0003) but not for commuting activity ($F_{[2]} = 1.2$, $p = 0.3$). Commuting and foraging activity levels were significantly greater in riparian than in upland forested habitat for all three elevational zones (Figs. 1 and 2). For all elevations combined, bat activity was 10.8 (commuting) and 40.2 (foraging) times greater in riparian than in upland areas. Commuting activity at upland sites (Fig. 1) and foraging activity at riparian sites (Fig. 2) decreased significantly with increasing elevation. Likewise, commuting activity at riparian sites (Fig. 1) and foraging activity at upland sites (Fig. 2) generally decreased with increasing elevation, although not significantly.

Capture

We operated mist nets in 1993, 1994, and 1995 for a total of 1340.6 mist-net hours, which resulted in 226 captures. Individuals belonging to nine species were captured: 58 *M. californicus*; 26 *M. evotis*, 53 *M. lucifugus*, 1 *M. thysanodes*, 16 *M. volans*, 56 *M. yumanensis*, 6 *E. fuscus*, 9 *L. noctivagans*, and 1 *L. cinereus*. Numbers of bat captures, with mist-net hours in parentheses, within each elevational zone were as follows: low, 179 (1037.8); mid, 47 (302.8); and high, 0 (49); and within each habitat type were as follows: riparian, 135 (452.5) and upland, 91 (888.1).

Bats were captured significantly more often in riparian than in upland areas for all sex and age classes (adult females: $\chi^2 = 33.78$, $df = 1$, $p < 0.001$; adult males: $\chi^2 = 7.9$, $df = 1$, $p < 0.01$; juveniles: $\chi^2 = 9.0$, $df = 1$, $p < 0.01$; Fig. 3). Adult females were captured significantly more often than adult males in riparian areas ($\chi^2 = 10.3$, $df = 1$, $p < 0.01$) but at similar rates in upland areas ($\chi^2 = 0.01$, $df = 1$, $p > 0.1$; Fig. 3).

Total bat captures per mist-net hour did not differ significantly between the low and mid elevational zones ($\chi^2 = 0.19$, $df = 1$, $p > 0.05$). However, reproductive and sex classes differed across elevational zones (Fig. 4). Adult females of both reproductive classes (P/L or NP/PL) were captured significantly more often in the low than in the mid elevational zone (P/L: $\chi^2 = 9.52$, $df = 1$, $p < 0.01$; NP/PL: $\chi^2 = 5.20$, $df = 1$, $p < 0.05$; Fig. 4). In contrast, adult males were captured significantly more in the mid than in the low elevational zone ($\chi^2 = 7.20$, $df = 1$, $p < 0.01$; Fig. 4). The capture rate of juveniles did not differ significantly between

Fig. 3. Sex and age class distribution (adult females, adult males, all juveniles) of bats captured in riparian and upland habitats (1 mist-net hour = one mist net operated for 1 h). An asterisk denotes a significant difference between riparian and upland habitat within sex and age classes ($p < 0.05$).

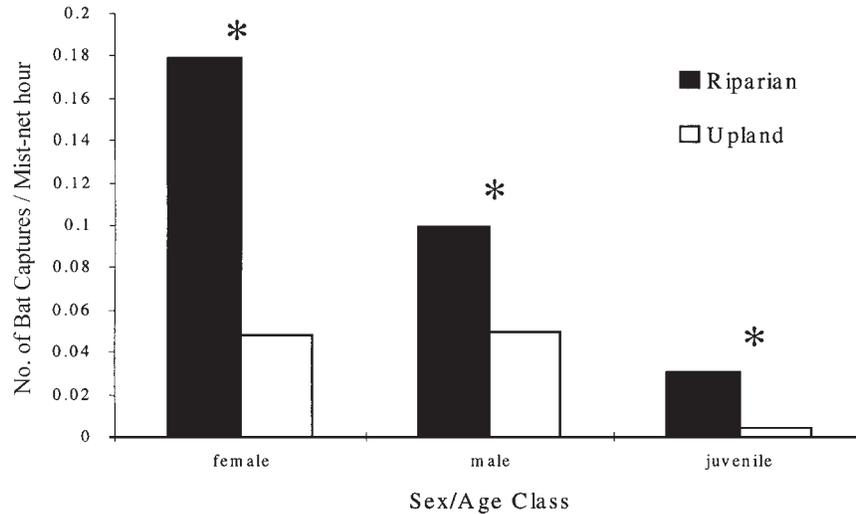
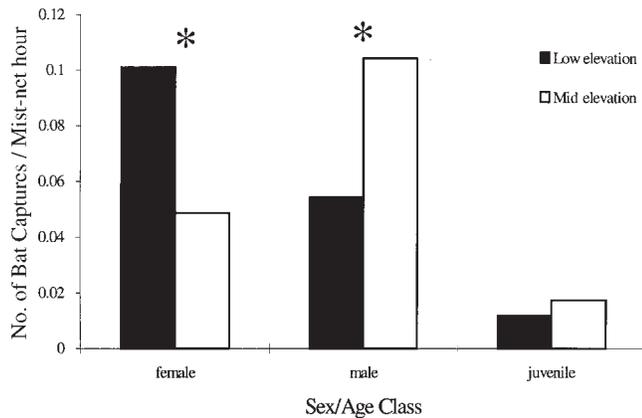


Fig. 4. Sex and age class distribution (adult females, adult males, all juveniles) of bats captured in low and mid elevational zones (1 mist-net hour = one mist net operated for 1 h). An asterisk denotes a significant difference between elevational zones within sex and age classes ($p < 0.05$).



the low and mid elevational zones ($\chi^2 = 0.92$, $df = 1$, $p > 0.05$; Fig. 4).

Discussion

Riparian and upland effects

As we predicted, riparian areas in our study area were important centers for bat activity relative to upland areas. We recorded significantly more foraging and commuting activity, and a greater number of captures, in riparian areas than in upland areas. Of special note was the substantially greater number of feeding buzzes in riparian habitats relative to upland areas. So not only was overall activity greater, but more importantly, foraging activity was significantly greater, in riparian areas.

Habitat structure and prey availability are known to influence habitat selection by bats (Fenton 1990; Grindal 1996; Brigham et al. 1997). Because of the similar physical struc-

ture (i.e., degree of spatial clutter, nature of the edge habitat) of the two habitat types (lakes and cutblocks) we studied, the 40-fold increase in foraging activity in association with lakes was presumably related to greater prey availability, as is suggested by other studies (e.g., Geggie and Fenton 1985; Brigham et al. 1992; Rautenbach et al. 1996). Flying insects that emerge from the surface of water bodies likely represent a plentiful and predictable supply of prey for bats. In addition, calm bodies of water provide suitable drinking sites for bats.

Riparian areas may be particularly important foraging areas for adult females. Assuming an equal sex ratio in temperate-zone bat communities (but see Kurta and Matson 1980), the larger number of adult females captured in riparian areas supports the notion that they actively select this habitat in which to forage as a response to the energetic demands of reproduction (Barclay 1989). Furthermore, Wilkinson and Barclay (1997) suggested that reproductive females may be territorial and actively force males into nonriparian areas. This would account for the fact that females were captured more frequently in riparian areas. Other possibilities that may explain the higher capture rates of reproductive females include the following: (i) these bats are more active because of their higher energetic demands and are thus more likely to be captured by chance; (ii) pregnant females are more susceptible to being captured, owing to the additional body mass associated with pregnancy, which reduces manoeuvrability (Kalcounis and Brigham 1994); and (or) (iii) females require higher levels of nutrients (e.g., calcium; Barclay 1994) that may be more easily obtained in riparian habitats.

Elevational effects

We expected that the reproductive, sex, and age classes of bats would vary with elevational zone as a result of differences in reproductive and thermoregulatory strategies (Fenton et al. 1980; Thomas 1988; Barclay 1991; Hamilton and Barclay 1994). Our capture data support this hypothesis, as we found a sex bias between the low and mid elevational zones. Adult males were captured more frequently in the higher

and cooler mid elevational zone, while adult females (both breeding and nonbreeding) were more common in the lower, warmer zone. Nonbreeding adult females may not have exhibited the predicted trend towards greater abundance in the mid elevational zone, as this group may have included pregnant individuals that could not be identified as such at the time of capture. Weaned juveniles of both sexes may also be expected to be more common at higher elevations in order to minimize energy expenditure through the use of torpor. However, juveniles may remain at lower elevations to take advantage of greater prey resources (necessary to accumulate fat for hibernation) or to maintain maternal contact. These confounding factors, as well as the low sample size of juveniles ($n = 7$), likely masked any trend that may have existed.

Relatively little foraging activity and no captures were recorded in the high elevational zone, while greater activity and capture rates were recorded in the mid and low elevational zones. Greater foraging activity and capture rates at lower elevations are likely the result of greater prey availability (Grindal 1996) as a result of higher air and water temperatures, which facilitate growth and development of the aquatic larval stages of some flying insects (Huffaker and Rabb 1984). Alternatively, higher foraging activity levels and capture rates in the low elevational zone may reflect the presence of buildings and lights along Kootenay Lake, which may have artificially increased the bat populations.

The relatively equal levels of commuting activity observed at riparian sites among the elevational zones likely also included drinking activity by bats. The lakes at which bat activity was monitored represent the few large bodies of still water available in this forested area. Small fast-flowing streams were available, yet these areas are probably unsuitable for foraging or drinking, owing to physical clutter and the high levels of noise produced, which interferes with bat echolocation (von Freneckell and Barclay 1987; Mackey and Barclay 1989). Bats roosting in higher elevational zones may travel to drink at these lakes, then commute to other, more profitable areas (e.g., lower elevations) to forage. Alternatively, if traveling to lower elevations to forage is energetically costly, greater commuting activity relative to foraging activity in the high elevational zone may reflect the greater effort (number of commuting passes/foraging attempts) necessary to encounter the presumably lower numbers of aerial insect prey at higher elevations. Although no insect sampling was conducted directly in relation to this study, a concurrent study in the same area showed greater insect availability (abundance, biomass, and species richness) in association with cutblocks in the low elevational zone than in cutblocks in the mid and high elevational zones (Grindal and Brigham 1999).

Our results represent a clear quantitative evaluation of the assumption that riparian areas are important for bats. If the lakes in our study area are indicative of the general trend, riparian areas are especially important centers of feeding activity by female forest-dwelling bats. Therefore, lake habitat, and most likely other riparian areas, need to be managed accordingly. In addition, our results indicate that inclusion of riparian areas is especially important when surveying for bats, and that sex and age class biases and relative activity

levels should be considered when sampling in different habitat types or over elevational gradients.

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